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ON SOME EARTHWORMS OF EISEN'S COLLECTION[1]

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Gustav Eisen, pioneer of oligochaetology in North America, and for whom three genera and several species were named, collected in California and Mexico, and also during 1880–1903, while he was on expeditions to Central American republics. Most of his material was lost at the time of the San Francisco earthquake in 1906. Fortunately, a few lots survived the disaster. The present contribution reports on those belonging to the California Academy of Sciences. This material was received by the author more than ten years ago. All of it is more or less softened. Some specimens were so macerated that even identification to family was impossible. Others were identifiable, but disintegrated more or less completely during dissection. The study of worms in such delicate condition is tedious and the results are not always commensurate with the time expended. However, some of the material has provided information of considerable interest.

The author's thanks are extended to Dr. Robert C. Miller for loan of the material. Especially appreciated is his understanding of the fact that a study of some of these specimens would result in their destruction.

On Certain Blood Vessels of Earthworms

Vascular organs were not mentioned in many of the specific descriptions, and in others only the location of the last hearts and the condition of the dor-

1. From research financed by the National Science Foundation.

sal trunk (whether double or single) were stated. Such inadequate treatment of essential structures is doubtless responsible for part of the artificiality of the classical system. Much more information must be obtained before taxonomic and phylogenetic importance can be evaluated, but data even now available suggest that certain vessels can provide characters for definition of more natural taxa, and of course for a better understanding of evolution.

Dorsal and ventral trunks are more likely than not to be complete, but abortions of short portions are known to be noteworthy in the octochaetid *Eutyphoeus*. Extra-esophageal trunks, free in coelomic cavities of a preintestinal region of the body, may prove to be uniformly median to or lateral to the segmental commissures and the hearts in some genera and this is even true in some families. Posterior portions of these trunks, by their associations with the esophagus and other major vessels, are expected to provide a greater diversity of taxonomic characters. Latero-parietal trunks (*cf.* Gates, 1939), in contrast to the extra-esophageals, are on the body wall throughout nearly all of their lengths, rising into the coelom only in some anterior segment to pass up toward the esophagus. Again, association with the gut or other major vessels may provide important characters. These trunks, like the subneural, often are empty or nearly so throughout most of their lengths, and then may be almost if not quite unrecognizable in field-preserved material. Posterior latero-parietals in *Eutyphoeus*, as well as in the octochaetid *Eudichogaster*, do pass back to the hind end of the body and, according to evidence now available, are present only when a subneural is absent. Anterior latero-parietals, possibly even two pairs, have been detected only in *Sparganophilus* in which a subneural appears to be lacking. The subneural has been thought to end in the vicinity of xiii–xiv, but probably is complete and continued to a bifurcation at the anterior end of the body.

Almost a century ago the segmental commissures or hearts that connect dorsal and ventral trunks were designated as laterals by Perrier. Hearts that connect supra-intestinal and ventral trunks he called intestinals. The term "latero-intestinal" was later coined by Bourne for hearts that open above into dorsal and supra-intestinal trunks. The supra-intestinal trunk of early authors long has been more properly called the supra-esophageal, and substitution of esophageal for intestinal in the Perrier-Bourne terminology (Gates, 1939, pp. 153–154) provided a more accurate characterization that was not so different as to require a glossary.

Latero-esophageal hearts have been identified by various authors as dorso-esophageals, true intestinals, intestinals, dorso-supra-intestino-ventrals, and esophageals. Lateral hearts have been designated as dorso-ventrals and esophageals. Esophageal hearts have been called intestinals, supra-intestino-ventrals. The terms lateral and esophageal have also been used for any heart, regardless of its dorsal connections. Unfortunately, the meaning of a par-

ticular characterization is not always determinable from the text or figures. Doubtless some of the confusion is attributable to the fact that one of the two dorsal bifurcations of a latero-esophageal heart is often empty. When strongly contracted, or in poor preservation, an empty bifurcation may be very difficult to identify. Possibly only in *Sparganophilus* are hearts present in an intestinal region of the body, but in that genus the vessels are lateral.

Family ACANTHODRILIDAE

This family now comprises the Acanthodrilinae of the classical system (*cf.* Gates, 1959), the holonephric genera of the Diplocardiinae (*cf.* Pickford, 1937), and the holonephric genera with tubular prostates of ectodermal origin that previously were in the Megascolecinae.

The classical Acanthodrilinae probably did not constitute a natural group as Stephenson seems to have suggested when he wrote (1930:819) that "convenience is best served" by placing therein all genera ineligible for admission to other megascolecid subfamilies. Recent additions (Gates, 1959) to the family admittedly were for convenience only. Not until much more information about previously neglected somatic anatomy is available will a more natural arrangement of genera into subfamilies or families be possible.

Genus **Plutellus** Perrier, 1873.

This classical genus includes species with one gizzard, in v, vi, or vii, that may be vestigial or well developed, sometimes even in two segments, v–vi or vi-vii and then really two. Species without calciferous glands or with glands of unknown structure which may be 2 pairs in xiv–xv or xv–xvi, 3 pairs in x–xii, or xi-xiii, 4 pairs in x–xiii or xii–xv or xiii–xvi, 5 pairs in ix–xiii. Species with an intestinal origin in xiv, xv, xvi or xvii, with hearts in x–xi, x–xii, x–xiii, the last pairs latero-esophageal, lateral, or even esophageal. By definition, the two prostates open to the exterior in xviii but in some species the prostatic pores are in xix or xx. Male gonoducts open to the exterior in xviii near the prostatic pores or pass into prostatic ducts within the body wall, just above the parietes, at various more ental levels to the end of the duct or even into the gland itself.

Plutellus, accordingly, is a congeries which has in common only the two characters of its family and in addition the lumbricin arrangement of the setae. The distribution, as incongruous as the morphology, comprises Ceylon, India, Burma, Australia, Tasmania, New Caledonia, New Zealand, Auckland Islands, Queen Charlotte Island, a Pacific coastal strip of the United States, Guatemala, and a northern portion of South America. The type species, supposedly from Pennsylvania, may not even be American. The andry is unknown and the holotype, though still in existence, seems never to have

been re-examined nor has the species been recognized elsewhere. Until *P. heteroporus* is more adequately characterized and some at least of its relationships are determined, perhaps more especially to North American species, the status of Eisen's *Argilophilus* is likely to remain uncertain. Accordingly, the commonly accepted classical generic name is retained for the two species considered below.

Plutellus papillifer (Eisen, 1893).

Plutellus papillifer, Gates, 1941, Proc. California Acad. Sci. 23, p. 443.

Colony Mill, Tulare County, California, 5415 feet, May 18, 1904, 0–1–0. Chas. Fuchs.

Tamalpais, Marin County, California, 0–2–10.

Tamalpais Station, Marin County, California, 1–2–18.

Eisen collection, no. 595, 0–0–2 (anterior fragments of 18 and 24 segments).

External characteristics. Diameter 6–7 mm. (fragments), 4–5 mm. (other specimens). Segments, 139–147, 161 (Colony Mill). Prostomial tongue open posteriorly but with a transverse furrow (several specimens) slightly behind the anterior margin of segment i. Ventral setae of ii are lacking (fragments) and follicle apertures either are closed or are now unrecognizable. Setae in preclitellar segments are ornamented near the tip with fine, transverse serrations.

Clitellum in xiii–xviii, anterior border indistinct, often apparently in xii, definitely at eq/xii (1 specimen) or much nearer 11/12 (1 specimen), in a third worm possibly at 11/12. The clitellum is protuberant (relaxed worms) or concave like a waist (some relaxed and contracted specimens).

Spermathecal pores at *B* (see notes to key below), except as indicated to the contrary in the section on polymorphism, at 7/8–8/9.

Female pores in a transversely elliptical area of epidermal thickening in *BB* which is opaque and protuberant except in one fragment where it is wholly translucent and depressed.

Male fields more or less distinctly demarcated, reach into xvii, as well as xix and are centered in *AB*. Each is longitudinally placed, widest at eq/xviii where a slight protuberance bears the male pore and follicle apertures. The epidermis in an anterior portion (mostly in xvii) and in an equisized posterior portion (mostly in xix) appears to be thicker but without translucence.

Genital markings are located as follows: 8/9 (14 specimens), 9/10 (33), 10/11 (34), 11/12 (33), 12/13 (32), 13/14 (4), 14/15 (34), 15/16 (33), 16/17 (24), 17/18 (3), 18/19 (1), 19/20 (33), 20/21 (28), 21/22 (8), 22/23 (1), 23/24 (1). A central portion of each marking is translucent except on

specimen no. 17 which has two discrete translucent areas in each of the markings from 12/13 posteriorly.

Internal Anatomy. Septa 5/6 and those following are funnel-shaped and so large that the gizzard is back at the level of the eighth segment, 6/7–10/11 increasingly thickened posteriorly, 11/12–12/13 decreasingly so, subsequent septa also slightly strengthened as is the horizontal subesophageal mesentery in x–xiii. A special longitudinal muscle band at mD is unrecognizable, but behind the clitellum in these relaxed worms a spindle-shaped gap in the longitudinal musculature extends a quarter of the way through each segment from the intersegmental levels between.

Gizzard large, strong, with thickened cuticular lining, in v (30 specimens). The ventral typhlosole always is obvious in x-xiv even in the fragments in which the mucosa has disintegrated. Low longitudinal ridges on inner wall of gut in x–xiv are irregularly interrupted. Esophageal valve short, at region of insertion of 16/17. Intestinal origin in xvii (20 specimens) and recognizably so even when the valve is relaxed. Typhlosole rudimentary but very gradually increasing in height through xxi to region of xxvi–xxviii, ending as follows: in 101st of 139 segments, 107th of 145 segments, 108th of 143 (abnormal worm), 144 and 146 segments, 110th of 147 segments, leaving 35–38 metameres atyphlosolate.

The dorsal trunk is complete, traceable in five worms to the brain underneath which it bifurcates, the branches passing ventrally along the circumpharyngeal nervous connectives. A supra-esophageal trunk is present in x–xiii. Extra-esophageal trunks always are median to the hearts and segmental commissures. Posterior lateroparietal vessels small, recognizable only in xviii–xiv of three specimens, pass up to the gut just in front of 14/15 but are not traceable to any of the major trunks. Segmental commissures of v–ix lateral, those of v in front of the gizzard, traceable to the ventral trunk only in viii-ix except in one worm and then in vii-ix. Last hearts in xiii (30 specimens).

Nephridia avesiculate, present from ii, in preclitellar segments of contracted specimens coiled in long and tight spirals.

Holandric and metagynous (except as noted below), male funnels rather small, plicate. Male gonoducts without epididymis, apparently united just in front of 12/13, passing into the prostate gland or somewhat more ectally and then at the junction of the duct and gland, sometimes with variation from one side to the other of the same worm. Seminal vesicles medium-sized or smaller, vertically placed on the posterior faces of the septa, acinous, not filling the coelomic cavities of xi-xii. Lumen of prostate glands slit-like in cross section, in the ducts much smaller and circular in section. Ducts 2 + mm. long, a slenderer ental portion with one or two u-shaped loops.

Penisetal follicles conspicuously protuberant into coelomic cavities and reaching to the middle of the prostatic duct or (an early aclitellate worm) to a level three-fourths of the way up the duct.

Spermathecae large, in contact with the ventral parietes back to the septum and then up on its anterior face, the appearance of a slight curvature presumably due to a greater elongation of the anterior wall of the duct. Ovaries fairly large, fan-shaped, with numerous short egg strings. Mature ova distinguished, in present condition of these specimens, by an obvious opacity that is lacking elsewhere in the gonad.

Genital polymorphism. Three specimens are of athecal morphs, even rudiments of spermathecae lacking as was demonstrated by removing the longitudinal musculature from the interior of the body wall. Each specimen is of a different morph. One worm (no. 33) has a small ovary but no female funnel on the right side of xiv and a testis but no male funnel on right side of xii. Differences between the other specimens are in genital markings and penial setae. The markings of no. 31 are at 9/10–10/11 and 14/15–20/21. Ventral follicles of xviii are only slightly larger than in adjacent segments. Shape and ornamentation of the setae are unknown as only middle fragments of setal shafts were found. (Each fragment was enclosed in a sleeve of cuticle that extended for some distance beyond the jagged edges, the setae possibly broken as the follicles were pulled out of the parietes.) Genital markings of no. 32 are at 9/10–12/13, 14/15–16/17, 19/20–20/21. Penial setae are as usual in sexual specimens.

First order intermediate morphs (*cf.* Gates, 1956, for terminology) are represented in the present lots by five individuals. One of these (no. 34) has four very small spermathecae that protrude into the coelomic cavities just enough to permit distinguishing the duct and ampulla. The spermathecal duct is slender and shorter than the ampullary rudiment. Penial setae of this worm are as usual. Ovaries and prostates are mature though a clitellum is as yet unrecognizable. A more advanced stage of evolution was shown by six of the seven worms previously examined (Gates, 1941, p. 449) in which ental ends of rudiments were just recognizable at the parietes. No indications of the differentiation of the duct and ampullary portions were recognized. In such evolutionary lines all spermathecae appear to have been simultaneously and equally affected. Whether further growth had been inhibited at an early stage of development or whether initial invagination had been too long delayed remains to be learned.

Two specimens lacked one of the posterior spermathecae, that on the left side. No rudiments were present at the sites of the missing organs. A quadrithecal individual, in which the right posterior spermatheca is shorter as well as slenderer than the others and without differentiation into duct and ampulla, may provide a somewhat earlier evolutionary stage.

Three worms are bithecal. One of the antero-bithecal (spermathecal pores at 7/8 only) individuals is juvenile. Spermathecae (of no. 36) are rudimentary and only slightly protuberant into the coelom. The prostates are fairly large but obviously are juvenile as are the testes, ovaries, and gonoducal funnels. Genital markings are not distinguishable (anlage possibly not visible because of poor condition?). The penisetal follicles, however, have attained adult size and the penial setae have the usual shape, size and ornamentation. The other antero-bithecal worm (no. 29) is adult but follicles of the ventral setae in xviii protrude only slightly into the coelom. The setae are penial but shorter and slenderer than usual and with somewhat coarser ornamentation. The postero-bithecal worm (no. 30) appears to be normal except for the absence of the anterior spermathecae.

Four worms are pseudo-intermediate morphs, so-called because they are not evolving in the direction of any of the major standard morphs such as A, R, and AR. Three worms (nos. 14, 24, 28) have an extra spermatheca on the right side of vii. The other (no. 25) has the extra organ on the left side. Each extra-spermatheca is normal (as are the other structures) except in no. 14 where the ampulla is only about one-quarter the usual size. Genital markings are located as follows: at 8/9–11/12, 14/15–15/16, 19/20–20/21 (no. 14), 9/10–12/13, 14/15–15/16, 19/20–20/21 (no. 24), 8/9–12/13, 14/15–16/17, 19/20–21/22 (no. 25), 9/10–12/13, 14/15–16/17, 19/20 (no. 28).

Addition of extra organs to a normal complement is much less common than deletion in genital polymorphism. The number of genital markings in these morphs of *P. papillifer* averages somewhat higher than in normally quadrithecal worms. Certainly there is little indication of deletion of markings, and in some lines markings may have been added.

No indications of any trend toward elimination of prostates or of precocious abortion of testes were detected. Aside then from reduction and elimination of spermathecae, reduction (and possibly elimination) of penial setae, the evolutionary trends that were noted are toward increase in number of spermathecae and of gonads. The extra gonads represent a return to an ancient ancestral condition, but addition to the spermathecal battery appears to be a change never before made in the ancestry of *P. papillifer*.

The ovaries seem to have matured precociously in an aclitellate specimen and may have done so in several clitellate individuals. The testes in some clitellate worms are very large, bushy, each of the numerous long digitiform lobes showing only the same early stage of spermatogenesis. Perhaps some modification in a system of endocrine control had delayed the initiation of male gametogenesis until it was too late for the sperm to be matured prior to breeding.

Abnormality. All organs of the left side from the first spermatheca back to the prostates are two segments behind their normal locations. Displace-

ments are due to intercalations of two metameres by halving of two mesoblastic somites at levels in front of the eighth (*cf.* Gates, 1960). Metamerism is abnormal in the region in front of what normally would have been 9/10. Genital markings are at 9/10–12/13, 15/16–16/17, 20/21–21/22.

Reproduction. Iridescence on the male funnels of the Tulare specimen proves that sperm had been matured. Iridescence within the seminal chambers in the spermathecal ducts shows that copulation had been completed even though a clitellum is lacking. Reproduction in this specimen presumably could have been biparental. Maturation of sperm, even profusely, does not, however, guarantee that reproduction is biparental (*cf.* Gates, 1957). Even after copulation reproduction may be parthenogenetic.

Spermatozoal iridescence was lacking on the male funnels and in the spermathecae of 29 specimens regardless of the condition of clitellum and ovaries. The breeding season for *P. papillifer* is unknown, and even if it were, collection dates are lacking for most of these worms. Mere absence of spermatozoa, in these circumstances, scarcely provides trustworthy evidence as to method of reproduction in most quadrithecal individuals.

Evolution of genital polymorphism obviously is well advanced in *P. papillifer*. This sort of polymorphism in earthworms appears, so far as now known, only when reproduction has become parthenogenetic. Individuals of athecal and of some of the intermediate morphs must reproduce parthenogenetically. Male sterility is anticipated in some of the quadrithecal worms with normal anatomy.

Remarks. Most of the specimens probably had been scoured, then anesthetized and preserved in a relaxed state. All now are more or less softened. The worms from which the anterior ends had broken off probably had been suddenly killed and preserved in such strong alcohol as to make them brittle.

Flocculent masses of corpuscles filled the coelomic cavities of most segments in the anesthetized worms. These masses may mask structures such as nephridia so that preservation is not as good as is needed for some studies. Presence of quite some amounts of the flocculent material in the coelom of v–vi was, in the present case, advantageous as it enabled easy recognition of the delicate septum 5/6 and its insertion on the gut just behind the gizzard. The septum is, however, attached at several points to the anterior margin of the gizzard which might, in less fortunate conditions, have been thought to be in vi (*cf.* notes on several species of *Ramiellona* below).

Except as indicated to the contrary above, the external characteristics and internal anatomy of each worm are as in previous specimens (Gates, 1941).

Hearts, of course, never were found in xiv. Possibly much distended anterior portions of the posterior latero-parietal trunks rising from the body wall of xiv were mistaken by Eisen for hearts.

Relationships with *P. marmoratus* remain to be worked out.

Plutellus marmoratus (Eisen, 1893).

Eisen Collection, 0–0–2. (No further data.)

External characteristics. Length, 80–83 mm. Diameter, 4 mm. Segments, 140, 167. Setae, $AA =$ or $< BC$, DD ca. $= \frac{1}{2}C$ anterior to clitellum, posteriorly $AA > BC$ or CD, $DD < \frac{1}{2}C$. Dorsal pores unrecognizable. Clitellum on xiii–xix/2 or xix. Females pores at A, midway between 13/14 and eq/xiv, within a transversely elliptical presetal tumescence in BB. Male fields distinctly delimited, reaching to presetal secondary furrow of xix and the postsetal of xvii, median margins especially tumescent.

Genital markings small and not quite as wide as AB, circular, each with a single greyish translucent central area, centered about at A, paired, at 9/10, 15/16 (1 specimen only), 16/17, 19/20.

Internal anatomy. Gizzard probably in v (2 specimens) but 5/6 very delicate, possibly incomplete and apparently attached (but not inserted) or perhaps only adherent at several points to anterior margin of the gizzard. Gut valvular in xvi–xvii, and there scarcely if at all thicker than the distended dorsal blood vessel, gradually widening in xviii–xx, normal intestinal width attained only in xxi. Typhlosole rudimentary in xix–xxiii, fairly high and simply lamelliform from region of xxiv–xxvi posteriorly, ending abruptly in 110th of 140 and 127th of 167 segments.

Last hearts in xiii (2). Nephridia avesiculate, ducts pass into parietes at C, D or, occasionally, dorsal to D by a distance about equal to CD.

Spermathecae fairly large, erect in coelomic cavities and reaching up to dorsal parietes. Duct much shorter than ampulla, wider entally and there with a considerable protuberance (almost reniform) from anterior and median face or from anterior half and in which a number of small seminal chambers are visible.

Reproduction. Irideseence on the male funnels of each specimen shows that sperm had been matured. Seminal chambers of two spermathecae of one specimen and all chambers of the other specimen contain sperm. Spermathecal ampullae are filled with a loose coagulum. As sperm are matured and then exchanged during copulation reproduction is assumed to be biparental. The worms may have been collected toward the end of breeding period.

Remarks. The specimens were macerated and fell apart during the dissection. The coelomic cavities of x–xi were filled with a compact coagulum

that came away with difficulty from the male funnels. The tips of penial setae are lacking or softened and deformed.

Except as indicated to the contrary above these worms are like *P. papillifer*.

Family OCTOCHAETIDAE

This family now comprises the Octochaetinae of the classical system (*cf.* Gates, 1959), the meronephric genera of the Diplocardiinae, and the meronephric genera having tubular prostates of ectodermal origin that were previously in the Megascolecinae.

The octochaetids of Mexico and Central America have been referred, in the past, to seven classical genera: *Eodrilus*, *Acanthodrilus*, *Trigaster*, *Dichogaster*, *Howascolex*, *Ramiellona*, and *Ramiella*. Consideration of *Trigaster* and *Dichogaster* is deferred to a subsequent occasion. All of the other octochaetids belong in *Ramiella*. The necessity for placing a Central American endemic (Gates, 1957) in an Indian genus provided yet another demonstration of the artificiality inherent in a system based primarily on esoteric phylogenies.

Eisen's collection now provides some reason for believing that further information with regard to taxonomically important somatic characters of American, as well as of Indian species, will enable at least two American genera to be morphologically distinguished from *Ramiella*. Although the American taxa cannot be so defined at present, resurrection of the first available name may obviate some nomenclatural changes in the future.

Howascolex by definition is "purely meganephridial" in an anterior portion of the body. Meganephridial, in the classical system, implied that excretory organs are two per segment only and also that each has a preseptal funnel as well as a coiled postseptal body with an epidermal nephropore in the same metamere as the loops. This is the condition that characterized the Eudrilidae, Glossoscolecidae, Lumbricidae, Ocnerodrilinae, Acanthodrilinae, and some of the Megascolecinae which were all defined (Stephenson, 1930) as meganephridial. Other excretory systems have several pairs to several hundred micronephridia per segment. In more highly evolved meronephric systems, some micronephridia were found to be as large as, or even larger, than meganephridia. To indicate whether a large excretory tubule was or was not one of several meronephridia in a segment, some qualification was needed, and the primitive condition (one pair per segment) became known as purely meganephridial. American species, so far as can be determined, are meronephric and without holonephridia (as they should be called) in any region of the body. Accordingly, these species are excluded by definition from *Howascolex* in which there are "true meganephridia" (Stephenson, 1930:843).

Genus **Ramiellona** Michaelsen, 1935

The word *Ramiellona*, a modification of *Ramiella* which is based on a Hindu patronymic (Ram), by itself hints at the difficulties encountered while attempting to define, in the classical manner, an American taxon so as to distinguish it from an unrelated group of species endemic in the Indian peninsula. Similarities, expressed in the usual classical manner, actually are as follows: lumbricin setae, acanthodrilin male terminalia, one esophageal gizzard in a single segment, micronephridial. *Ramiella* lacks calciferous glands which means only that no pouches are constricted off from the gut. *Ramiellona* accordingly was distinguished by the presence of calciferous folds within esophageal widenings in xii and some of the preceding segments. Mention of esophageal widenings or of foldings of the inner wall cannot be expected in older descriptions as even highly evolved calciferous glands were derogated taxonomically. However, one Indian species, *Ramiella nainiana* Gates, 1945, does have in viii–xii (*cf.* descriptions below) folds between which calcareous granules were found. For the present, then, the two genera are distinguishable only by their geographical distributions.

The Guatemala specimens probably were quickly killed in the field and preserved in a strongly contracted state. Most are folded, twisted, or coiled. During their stay in alcohol their tissues were browned with the resultant loss of optical differentiation. Soaking in a solution of picric acid did improve matters somewhat, but not enough in several instances to permit characterization of the genital markings. The softening, usually associated with long stay of earthworms in any of the standard preservatives, obviates certainty as to the number of intestinal caeca and sometimes even as to presence or absence of these structures. The nephridia, of course, are in poor condition and microscopic structure was not determinable. Portions of the esophagus almost certainly are deformed in some individuals as a result of strong contraction. Extremes of deformation probably are recognizable, but states that seem more normal may not be recognizable after slight relaxation. Even before deterioration has set in, field preservation may not be good enough to permit detection of taxonomically important characters in the excretory system.

Ramiellona guatemalana Gates, new species.

Guatemala, vicinity of Totonicapan, highlands of Huehuetenango, May-Nov. 1902. 15–19–3. G. Eisen.

External characteristics. Length 140–190 mm. Diameter 5 mm. Segments, 287, 294, 320. Prostomium, prolobous (30 specimens), recognizable from dorsal side (3), visible in buccal cavity from anterior end (27), so deeply retracted as to be invisible from exterior (7). Peristomium soft, with

many longitudinal creases, some part (except in 3 specimens) withdrawn into the anterior end. Two furrows on the peristomium, next to mD, sometimes appear to be deeper than the others and then may look like margins of a tanylobous tongue. A deep transverse furrow, however, always demarcates the prostomium from the real anterior margin of i. Pigmentation unrecognizable (alcoholic preservation). A postsetal secondary furrow is present from iv posteriorly, a presetal secondary from viii. These secondaries in the preclitellar region, may be as deep as the intersegmental furrows so that recognition of the latter becomes difficult. Tertiary furrows behind the clitellum, slight, often apparently incomplete but scarcely distinguishable from the secondaries. Toward the hind end the segments are very short and without secondary annulation. Nephropores unrecognizable and doubtless microscopic. First dorsal pore at 12/13 (22), ?12/13 (2), ?13/14 (5), unrecognizable until behind clitellum (2 specimens).

Setae lacking in ii–iii (20 specimens), also absent in iv (7), *a* and *b* alone present on right side of iv (3), *c* and *d* often lacking on v or v–vi, at first very small and very closely paired. In front of the clitellum, $AB = CD$, $AA < BC$, DD ca. $= \frac{1}{2}C$, near the 37th segment CD becomes wider than AB, the lateral ranks very gradually becoming more irregular but only in region of the 150th segment beginning to get well into the dorsum. The size of the setae as well as the protuberance from the epidermis increases posteriorly and as the quincuncial arrangement is attained, but decreases again in the last 4–6 setigerous segments. The enlarged posterior setae are rather spindle-shaped, their tips ornamented with about 15 rather widely and irregularly interrupted circles of very fine serrations. Ventral setae of xvii and xix penial, usually markedly protuberant. Ventral setae of xviii present (37 specimens), seemingly displaced slightly toward mV, ornamented distally with short transverse rows of fine serrations at 15–20 circumferential levels, a shorter terminal portion curved slightly to one side.

Clitellum saddle-shaped, reaching down nearly to *B*, on xiv–xix.

Spermathecal pores transversely slit-like when closed, nearly circular when open and then filled with a plug of hard coagulum or revealing internally smooth and glistening anterior as well as posterior lips in contact with each other, in AB at 7/8–8/9. Female pores minute, in setal annulus of xiv, just in front of or slightly anteromedian or anterolateral to *a*. Male pores somewhat larger, transverse slits, in seminal grooves and just at 17/18. Prostatic pores immediately lateral to apertures of penisetal follicles, usually unrecognizable except when traction on adjacent epidermis separates the margins, about at equators of xvii and xix. The penial setae at first appear to emerge from a single aperture on each side of xvii and xix, but after they have been pulled out, a dividing membrane can be seen to reach down almost to the level of the external surface of the epidermis. Seminal grooves with

tumescent margins, well lateral to *B*, curve mesially in xvii and xix to the prostatic pores. An equatorial portion of xvii and xix, about at *AB* on each side, seems to be somewhat tumescent and is protuberant in a rather conical manner, follicle apertures at the apex. Seminal grooves and genital markings provide boundaries for a median male field that usually is slightly depressed.

Genital markings unpaired and median, transversely placed, the anteriormost often about reaching m*BC*, size decreasing posteriorly, along intersegmental furrows as follows: 16/17 (15 specimens), 19/20 (11), 20/21 (12), 21/22 (4). Posterior markings perhaps develop later than the one at 16/17 as they are lacking on the younger specimens. Each marking probably has one transverse row of circular areas. The equatorial annulus of xx and xxi (4 specimens), between the genital markings, is conspicuously protuberant, apparently somewhat tumescent and with a distinctive white opacity that is especially obvious because of the alcoholic browning in adjacent areas.

INTERNAL ANATOMY. Septa 5/6–9/10 large, funnel-shaped, posteriorly directed, 5/6 muscular, 6/7–9/10 thickly muscular, 10/11 slightly muscular, 11/12 obviously thicker, 10/11–11/12 united peripherally except ventrally in a middle portion of *CC* and organs of xi unrecognizable in a dissection from the dorsal side until after the apparently very thick septum 10/11 has been separated into its constituent parts. A special longitudinal muscle band at mD is present from 11/12 or 12/13 and is very distinct. Large and strong muscle bands from the posterior margin of the gizzard are inserted in the parietes of xi or xii. Diagonal muscle bands, with median parietal insertions near nerve cord, are present in xvi–xix; two in xvi on each side that are wide provide a useful marker for the segment, sometimes only one is present on each side but then it is much wider, covering the parietes from 15/16 to 16/17. A transverse muscle band from the gut in xiii passes, on each side, straight laterally to a parietal insertion.

Gizzard large and strong, with a thickened cuticular lining, in v (8 specimens), but because of the size of the septal funnels about at the level of viii–ix as indicated by intersegmental furrows externally. Postgizzard portion of esophagus narrow, high up in the coelomic cavities, little if any longer than the gizzard, or at most shorter than the section in i–v. Esophagus deeply constricted by 7/8–12/13, apparently with five pairs of sacs, the first two or three pairs gorged with blood so as to appear black, the last two pairs always white, the first two pairs apparently opening widely into the esophagus, the next three pairs more nearly constricted off, but without stalks and opening through smaller circular apertures. Calciferous lamellae numerous, thin, high, with free margins centrally, in viii–xii and possibly reaching very slightly into vii. Lower and rounded longitudinal ridges are present on the inner wall of the esophagus in xiii–xiv. Intestinal origin in region of inser-

tion of septum 14/15, apparently just in front of the insertion (4 specimens) or just behind (4)—septa 14/15–15/16 often in contact mesially and adherent to each other, an anterior portion of the intestine with insertions of one or both septa sometimes drawn back into the interior of the gut, the adjacent portion of the intestine then bulged forward. Intestinal caeca small, paired, arising just lateral to the level of the secondary typhlosole (which is indicated externally by a deep red band) and immediately behind the septa, in Rxxiii–xxvi (1 specimen), xxiv–xxvi (1), xxiv–xxvii (1), xxv–xxvi (1), xxv–xxviii (1), (xxiv–xxv?) xxvi–xxx (1) xxv–xxx (1), unrecognizable (1). Typhlosole rudimentary from xvi to region of xxii–xxiv, thence posteriorly fairly large, thicker distally and with three longitudinal ridges on its ventral face, ending abruptly in 162d of 287, 176th of 294, 168th of 320 segments. Lateral typhlosoles low but simply lamelliform, beginning and ending abruptly, uninterrupted, just median to the caecal apertures, from the region of xxii–xxiv to xxx–xxxii. Supra-intestinal glands lacking.

Dorsal blood vessel single throughout, complete, bifurcating just behind or under the brain, the branches passing ventrally along the circumpharyngeal nervous connectives to unite and become the ventral trunk (2 specimens). Ventral trunk complete, in front of 4/5 joined by three pairs of blood-filled vessels and then bifurcating over the subpharyngeal ganglia (3 specimens, in one of which the branches are traceable only a short way up the nervous connectives). Extra-esophageal trunks recognizable from ii, large and filled with blood anteriorly, median to segmental commissures, empty and not traceable posteriorly. Supra-esophageal trunk bound closely to gut in viii–xii, with a large branch to each calciferous gland of viii–xi, bifurcating anteriorly in xii. Commissures of vi–x lateral, traced to the ventral trunk except in vi, each joined just before opening into the ventral trunk by one or two vessels as large as itself. Commissures of v lacking or unrecognized. Hearts of xi–xii latero-esophageal, anterior bifurcation of a heart of xii continuous with posterior bifurcation of the supra-esophageal. Subneural trunk not found (7 specimens) and probably lacking. Latero-parietal trunks not found.

Excretory system meronephric. A longitudinal band of closely crowded micronephridia is somewhat lateral to mV on each side in iii–iv. Two ducts emerge together from the anterior margin of the cluster, but separate almost at once and disappear from view on parietes of ii and iii. Smaller clusters of nephridia are present on the anterior faces of 4/5–11/12 or 12/13. One cluster usually is recognizable way up on the septum alongside the gut. Another cluster joins the duct which runs downward on the septum, near the ventral parietes. Nephridia are at the parietes from one of segments xii–xv but at first the loops are vertical against anterior faces of the septa, from xx posteriorly the tubules are arranged in a transverse row at the middle of each

segment. At least five longitudinal ranks appear to be present on each side of the body (crowding and poor condition of the organs obviating more precise characterization). The median nephridium on each side in a posttyphlosolar region of the body is no larger than some others in the same segment, but it does have a preseptal funnel.

Metandric (7 specimens), testes of xi bushy, male funnels large and plicate, the testicular chamber (formed by peripheral union of 10/11–11/12) containing more or less coagulum but no seminal vesicles. Male funnels of x rather small but plicate (no testes in x). Seminal vesicles finely acinous, one pair, filling the coelomic cavity of xii, at maximal development bulging pockets of 12/13 back into xiii or xiv or (1 specimen) rupturing 12/13 and penetrating into xiii where a number of the lobes are separated off (owing to maceration?). Male gonoducts without epididymis but sometimes shortly looped in xiii–xvi, with thick wall (presumably muscular but without sheen), slightly narrower in xvii and there lateral to prostatic ducts, passing down into the parietes in front of *a* of xviii. Slender ducts from male funnels of x are traceable (1 specimen) back to junctions with other ducts in xii. Prostates tubular, coiled in xvii and xix, distending septa or reaching into xix and xx–xxii, ducts with muscular sheen and 2–3 mm. long. A thick muscular sac containing follicles of functional penial setae projects conspicuously into the coelomic cavities just median to each prostatic duct. Reserve penial setae often occur in a membranous sac that passes back from the apex of the muscular sac. Penial setae red or with some greenish color in an ectal portion of the largest shafts, thick, 2–4 mm. long. Shaft nearly straight or in a slight arc like a parenthesis. Distally the shaft narrows abruptly or gradually, the tip band-like, curved over to one side and at low magnification often seemingly hook-shaped. The margins of the band usually are slightly curved toward each other, but when the narrowing is abrupt the short tip may have a shape more or less like that of the bowl of a spoon. Ornamentation is of 30 or more circles of fine serrations, irregularly and frequently interrupted. The teeth, on the tip, are fewer, coarser, and with pointed distal ends well away from the shaft.

Spermathecae fairly large, to 5 mm. long, reaching up to the level of gut on the anterior faces of the septa, adiverticulate and without external demarcation into duct and ampulla. The duct is the anterior vertical portion passing straight down through the body wall and is thicker than the ampulla. The narrow lumen of the coelomic portion of the duct curves over posteriorly. The long ampulla gradually narrows entally. The rather thickish wall is provided with numerous closely crowded annular ridges. The seminal chambers, 6–8, are in the thicker anterior wall of the duct. Ovaries fan-shaped, with several short egg strings, usually hidden against ventral parietes by muscle bands. Oviducal funnels slightly folded, readily recognizable.

Reproduction. Iridescence on the male funnels of three aclitellate and one clitellate specimens is brilliant. Iridescence also is recognizable in the spermathecal seminal chambers of the aclitellate worms, but was not distinguishable in two spermathecae of a clitellate specimen. Reproduction, inasmuch as sperm are matured and then exchanged in copulation, is assumed to be biparental.

Growth stages. Juvenile 2 mm. thick. The epidermis in *AB* at equators of xvii and xix appears to be slightly tumescent. The tips of the red setae are just distinguishable in a central depression of the tumescence. The testes (xi only, none in x) are bushy but seminal vesicles had not as yet appeared. The spermathecae just protuberant into coelom, slender but already bent over toward the posterior septa. The ventral follicles of xvii and xix are protuberant into coelom just enough so that they can be grasped with the fine forceps. Each follicle contained three red setae, one a mere tip, a second about half the length of the longest which has a ribbon-like and flat tip. The male funnels are recognizable in x as well as in xi, but are much smaller in x.

Larger juveniles possess more prominent tumescences in xvii and xix, but still lack seminal grooves.

More mature worms, with distinct seminal grooves, were listed as aclitellate. One such has no genital markings and may not have been mature enough for them to be recognizable. Testes, with early stages of spermatogenesis, are unusually large in one early aclitellate with quite juvenile prostates, male funnels and seminal vesicles.

Aclitellate worms with sperm in the spermathecae showed no signs of a clitellum having regressed, but the seminal vesicles are dark. Epidermal evidences of clitellar regression could have been unrecognizable because of alcoholic browning, but contrariwise the dark appearance of the vesicles could be due to the browning by alcohol and so not evidence for postsexual regression.

Autotomy. Three worms obviously are very recent posterior amputees. Two to seven circumferential constrictions, always at intersegmental levels, are recognizable, on several other specimens, in the terminal forty millimeters of the body. At some of those constrictions the body wall already had been ruptured on one side or the other. The species obviously autotomizes readily, perhaps rapidly and sometimes extensively. The stimulus to the rupturing, in the present instances, may have been provided by grasping the worm posteriorly to drop it into the preservative. Individuals of species that do autotomize readily never have done so, in the author's experience, in killing alcohol regardless of the strength employed. Autotomy then can be avoided by seizing the worm near the anterior end.

An anterior rupture through which spermathecae protrude (aclitellate specimen) is likely to have been produced by the instrument used for digging

(or perhaps ploughing) up the worms. Eight anterior fragments probably were broken off in that way.

Ingesta. Earth, reddish. No bits of plant matter were recognized under the binocular.

Abnormality. Spiral metamerism involving segments xi–xvi (1 specimen).

Parasites. Large, blood filled blisters of the intestinal wall in region of xvi–xxx contain two parasites each for which it is hoped identification can be obtained.

Remarks. Parietal insertions of some of the anterior septa almost certainly are displaced from their proper intersegmental levels. Two adjacent membranous septa sometimes adhere to each other so completely as to result in erroneous enumerations. Painstaking manipulation and repeated checks against fixed-position organs and against external annulation often were necessary. Even so, certainty as to the segment of intestinal origin was not achieved.

Some coelomic cavities were completely filled by a coagulum. No glands were recognized in the body wall above the genital markings.

Several characters, including retraction of the prostomium, location of the first dorsal pore, quincuncial arrangement of the setae, genital markings —identically located and each with a transverse row of circular areas, the trifid typhlosole, the ten ranks of nephridia in a postclitellar portion of the body, suggest relationships with the Salvadorean *R. lasiurus*. Differences, however, are numerous and as follows: prostomium prolobous (epilobous), clitellum saddle-shaped and on xiv–xix (annular on xiii–xx), muscularity of 5/6 (septum not mentioned), gizzard in v (vi), calciferous sacs in viii–xii (ix–xiii), segmental commissures and hearts in vi–xii (vii–xi), presence of a testicular chamber (not mentioned), metandric (holandric ? with seminal vesicles in xi?), spermathecae adiverticulate (with a sessile, rosette-shaped diverticulum). Guatemalan worms also appear to be slightly larger and to have more segments. Some of these supposed differences may be of little or no taxonomic significance (*cf. R. lasiurus* below) and the more important ones now appear to be those relating to the clitellum and to the spermathecal diverticulum.

To facilitate further discussion of relationships in this difficult group there are subjoined certain notes on those species of which no material has been available for study. Each of these forms, with one exception, is known only from the original specimens secured at a single locality.

Ramiellona balantina Gates, new species.

Guatemala, vicinity of Totenicapan, highlands of Huehuetenango, May-Nov. 1902, 0–3–0. G. Eisen.

External characteristics. Length, 116 mm. Diameter, 6 mm. (largest specimen). Segments 111 (old posterior amputee), 197, 203. Pigmentation not determinable (alcoholic preservation and considerable browning). Prostomium prolobous (2 specimens), withdrawn but visible from the anterior end or unrecognizable (third specimen). A postsetal secondary furrow is present from vi or vii posteriorly, a presetal secondary from viii or ix. Secondary furrows behind the clitellum, slight and scarcely distinguishable from the tertiaries. Setae possibly lacking in ii as well as iii (part only?), *a* and *b* of xvii–xviii present, *a* and *b* of xix penial, very small and very closely paired in preclitellar region, *AB* ca. = *CD*, *AA* < *BC*, *DD* ca. = ½C throughout much of the body, toward the posterior end *AB* and *CD* somewhat wider but only slightly smaller than *AA*, the *d* rank becoming somewhat above mL, all more protuberant and probably somewhat larger. Setae in the region of cxx ornamented with irregular interrupted circles of fine serrations, a short portion of the tip curved to one side so as to have a hook-shape. Nephropores unrecognizable and apparently microscopic. First dorsal pore, at 12/13 (2), ?13/14 (1).

Spermathecal pores, fairly large, centered about at *A*, one pair, at 7/8 (3 specimens). Female pores minute, just in front of *a* and hence in equatorial annulus of xiv (1). Male pores, somewhat larger, in seminal grooves, lateral to *B* at 18/19 (3). Prostatic pores at ends of the seminal grooves, just lateral to apertures of penisetal follicles, at eq/xix. The penial setae at first appear to project from a common aperture but after they have been drawn out a vertical membrane can be seen to reach down almost to the level of the external surface of the epidermis. Seminal grooves, lacking in the smallest specimen, pass from the prostatic pore anterolaterally to 18/19 (larger worm) or to 17/18 (largest specimen). Ventrum of xix to m*BC* markedly tumescent (3), reaching greatest elevation at *A* where there is a half-collar of special protuberance that is open laterally just beyond the penial setae.

Genital markings unpaired, transversely placed, recognizable only on the largest specimen and there at 15/16–17/18, 19/20–21/22. Each marking probably has one transverse row of circular areas.

Internal anatomy. Septa 5/6–9/10 large, funnel-shaped, posteriorly directed, 5/6 muscular, 6/7–9/10 thickly muscular, 10/11 muscular, 11/12 thickly muscular, 10/11 and 11/12 united peripherally except ventrally in region of *BB* so that organs of xi are unrecognizable in a dissection from the dorsal side until after an apparently very thick septum 10/11 has been separated into its constituent parts. Special longitudinal muscle band at mD

quite distinct. Large muscle bands from the posterior margin of the gizzard pass back to parietes in region of x–xii. A strong band from the lateral face of gut, on each side of xiii, has a parietal insertion laterally in xiv. Diagonal parietal bands, strong and wide, have median insertions near the nerve cord in xviii, but similar bands are lacking in xvi–xvii.

Gizzard large and strong, with thickened cuticular lining, in v (3 specimens) but about at level of viii–ix as indicated by intersegmental furrows externally, so elongated in one worm that its anterior opening is dorsal and its posterior aperture is ventral. Postgizzard portion of esophagus narrow, high up in coelomic cavities, little if any longer than the gizzard, deeply constricted at insertions of 7/8–12/13, the portions in viii–ix thin discs of nearly circular outline between compressing septa, a somewhat larger but equally thin disc in x obviously bilobed. Calciferous lamellae with free margins centrally, in viii–xii, of xi–xii within nearly spheroidal unstalked sacs all four of which at first appeared to be in xii as separating tissues are very thin. Intestinal origin in the region of insertion of 14/15, seemingly (3 specimens) just in front of 14/15. Intestinal caeca small, recognizable only with difficulty, in xxiv–xxv (3), possibly a smaller caecum in xxvii (1). Typhlosole rudimentary but lamelliform in xvi to region of xxii, thence posteriorly with widened ventral portion bearing three longitudinally lamelliform ridges, ending abruptly in 123d of 197 segments but in the amputee becoming rudimentary in the 94th segment and unrecognizable behind the 108th. Lateral typhlosoles low but lamelliform, uninterrupted, in xxii–xxviii. Supra-intestinal glands lacking.

Dorsal blood vessel single throughout. Extra-esophageal trunks empty and unrecognizable except anteriorly. Supra-esophageal trunk distinguishable only in xi–xii. Subneural trunk not found (2 specimens) and probably lacking. Lateroparietal trunks unrecognizable. Segmental commissures of vi–x lateral, traceable to ventral trunk only in x. Hearts in xi–xii, lateroesophageal.

Excretory system meronephric. A longitudinal band of closely crowded micronephridia parallels the nerve cord on each side of the body in iii–iv. Smaller clusters of micronephridia are present on the anterior faces of septa 4/5–11/12 or 12/13. Nephridia from xiii posteriorly, on the parietes, behind xx in at least four (possibly 5 or 6?) longitudinal ranks, the tubules transversely placed at the equator of each segment. The medianmost nephridium on each side, toward the hind end, has a preseptal funnel. Stomate nephridia of one specimen obviously are thicker than the astomate tubules of the same segment.

Metandric (3 specimens), testes (present only in xi) bushy, the testicular chamber with little or no coagulum but reaching forward (because of a ventral pocket of 10/11) on floor of x nearly to 9/10 (largest specimen). Male funnels all plicate, those of x smaller, those of xi (the largest specimen)

within the anterior pocket of the testicular chamber. Seminal vesicles finely acinous, one pair in xii. Male gonoducts without epididymis, united on each side in front of 12/13, seemingly with a muscular sheath though the sheen is unrecognizable, passing down into the parietes in the region of 18/19. Prostates in younger specimens obviously juvenile and coiled in xix, probably adult in the largest worm where they reach into xx. Ducts about 2 mm. long, muscular, looped. Penisetal follicles within two thick, muscular sacs conspicuously protuberant into coelomic cavity of xix. Membranous sacs passing back from the apex into xxiii, each containing a large and a small reserve seta as well, sometimes as a mere tip of a third. Penial setae (functional), 2 + mm. long, thick, sometimes widest at ectal end which sometimes appears to be rather bulbous and abruptly narrowed to a terminal spine. The latter, usually softened, reveals under high magnification the shape of a spoon bowl. Shafts of reserve setae lack the bulbous widening at the tip and may narrow gradually to a thin band. Ornamentation is of frequently and irregularly interrupted circles of fine serrations, the teeth slightly larger and rising slightly away from the shaft on the narrowed tip.

Spermathecal duct vertical, thick, wider entally, adherent to the posterior face of 7/8, with a rather flat dorsal surface. Ampulla of about the same size as the duct, on the ventral parietes, ovoidal, narrowing to a very short but still fairly thick neck that passes to the posterior face of the duct. The wall of the ampulla is opaque (not membranous) and without obvious ridges. The lumen is wide distally and filled with coagulum, but in the neck it is very small as in the duct. Six slight white rounded protuberances on the dorsal face of the duct anteriorly mark the sites of distended seminal chambers. One or two additional chambers may be present down deeper so as to be unrecognizable externally. Ovaries fan-shaped.

Reproduction. Iridescence on the male funnels of the largest worm is brilliant. The seminal chambers, in one spermatheca, are filled with a material in which iridescence is readily recognizable. Although there is no clitellum, the worm must have copulated. Reproduction, as sperm are matured and exchanged in copulation, is assumed to be biparental.

Ingesta. Earth, fine textured, dark, of a reddish brown color, without macroscopically recognizable plant fragments.

Parasites. Six nematodes, red except at each end, were found in the coelomic cavity of xii (1 worm). Several small white cysts are present on an anterior portion of the intestine.

Remarks. Protuberances from xix presumably can be inserted into the large spermathecal pores to function as temporary intromittent organs.

The short seminal grooves of the less mature worm are slight and may not have attained full development in depth as well as in length.

An esophageal typhlosole at mV, as in the previous and the next species, was not recognized.

Somatic anatomy indicates close relationships to species that are designated hereinafter as the "*guatemalana*" group. The major difference from others of the group (and which probably would have been considered very important in the classical system) is that the genitalia have undergone the metandric and the balantin reductions. The present species, accordingly provides one more demonstration that genital anatomy is liable to more rapid evolutionary modification than the somatic. The persistent male funnels of segment x show that advent of metandry was recent. Holandric individuals or even a holandric subspecies may be found. The balantin reduction of the ancestral acanthodrilin male terminalia is much rarer than the microscolecin and is as yet little known.

The peristomium, with numerous longitudinal wrinkles, is flaccid, a condition that appears not to be wholly attributable to postmortem softening, especially in view of the firmness of the prostomium. Apparently under way in the "*guatemalana*" group is an evolutionary derogation of the first segment which can be expected to result, perhaps in some hitherto uncollected species, in disappearance of intersegmental furrow ½. With loss of the setae of the next metamere, i and ii would be indistinguishable and all fixed-position organs would appear to be one level in front of their usual locations. Just such a change appears to have been completed in two megascolecid Indian genera, *Tonoscolex* Gates, 1933 and *Nelloscolex* Gates, 1939. A similar process is well under way in at least one species of the American glossoscolecid genus *Pontoscolex* Schmarda, 1861, in which 1/2 has disappeared but setae of ii still are present. The prostomium in *P. corethrurus* (Müller, 1856) seemingly has disappeared, but in *Tonoscolex* and *Nelloscolex* was retained. Retention of the prostomium now seems more likely to characterize more advanced stages of peristomial derogation in Central America.

Male apertures in the supposedly ancestral, acanthodrilin genitalia of the classical system are at eq/xviii, midway between the anterior and posterior prostatic pores which are at eq/xvii and eq/xix. Although all four glands appear to be equally developed (and presumably synchronously) in the "*guatemalana*" group, the male apertures are further anteriorly, at 17/18 and hence closer to the openings of the first pair of glands. Disappearance of the anterior prostates supposedly involves union of male and posterior prostatic pores. That has not happened in *R. balantina* where the male openings do not even get into xix, but are at 18/19 and so are at the same distance from the remaining prostatic pores as they previously were from the anterior pair.

Ramiellona strigosa Gates, new species.

Guatemala, vicinity of Totenicapan, highlands of Huehuetenango, May-Nov. 1902, 0–5–1. G. Eisen.

External characteristics. Length, *ca.* 97 mm. Diameter 3–3½ mm. Segments, 181, 203, 208. Prostomium prolobous, just recognizable from dorsal side (2 specimens), visible only from anterior end (4). Peristomium soft, with numerous longitudinal creases, some part withdrawn into anterior end (6). A postsetal secondary furrow is present from v, a presetal secondary from viii or ix. Tertiary furrows behind the clitellum, slight, often apparently incomplete and scarcely distinguishable from the secondaries. Setae present from ii, small, closely paired, *DD* ca. = ½*C* throughout, *AB* = *CD*, *AA* < *BC* anterior to clitellum, behind the clitellum *AA* > *BC*, toward posterior end *AA* and *BC* only a little larger than *AB* and *CD*, ventral setae of xvii and xix penial, ventral setae of xviii present (6 specimens) and median to seminal grooves. Nephropores unrecognizable and doubtless microscopic. First dorsal pore at 12/13 (6), in the clitellate worm a functional pore present at 13/14.

Clitellum dark red, intersegmental furrows obliterated, dorsal pores occluded, setae unrecognizable, probably at maximum tumescence, saddle-shaped, reaching down to *B* except in xvii–xix and there only to m*BC*, on xiv–xix, extending halfway through xx and slightly into xiii but in each of those segments much thinner and not so dark.

Spermathecal pores with rather irregular margins, not minute, centered about at *B*, two pairs, at 7/8–8/9 (6 specimens). Female pores minute, in setal annulus of xiv, slightly anteromedian to or just anterior to *a* (3). Male pores in seminal grooves, apparently at 17/18 (3, but location could not be confirmed by tracing male gonoduct through the musculature). Seminal grooves well lateral to *B*, pass mesially in xvii and xix onto conspicuous protuberances at apices of which are prostatic pores and follicle apertures.

Genital markings unpaired, transversely placed, each with a single transverse row of circular areas, at 10/11, 11/12 and 20/21 (2 specimens), 11/12 and 20/21 (1), in *BB* posteriorly, reaching into *BC* anteriorly, unrecognizable and presumably not yet developed (3 specimens). Areas of translucence and of about the same size, slightly depressed, may be present, on some specimens at 16/17, 18/19 and 19/20.

Internal anatomy. Septa 5/6–11/12 funnel-shaped and posteriorly directed, funnels of 5/6–9/10 especially large, 5/6 membranous but complete, 6/7–9/10 or 10/11 rather thickly muscular, 11/12–12/13 slightly strengthened. Special longitudinal muscle band at m*D* very distinct. Diagonal muscle bands broad, with median parietal insertions near nerve cord, present in xvi.

Gizzard large and strong, about at the level of viii–x as indicated by intersegmental furrows externally but actually in v (5 specimens). Postgizzard portion of esophagus slender, fairly high up in coelom, deeply constricted at the septal insertions. Calciferous lamellae fairly high and with free margins centrally, in viii–xii. Small, lateral sacs seemingly are present in each of vii–x, the sacs opening widely into esophageal lumen. Sacs in xi–xii more distinctly constricted off, though unstalked, and protruding slightly above and slightly below the median portion of gut. Intestinal origin in the region of the insertion of 14/15, almost certainly just behind 14/15 (1 specimen), apparently so but possibly not (the other four). Intestinal caeca indistinct, in xxiii–xxiv (3 specimens), apparently just in front of the septa, and in one worm recognizable only on the left side, in (xxiii?) xxiv–xxviii (1), xxiv–xxviii (1). Typhlosole rudimentary till region of xxii–xxiv, then abruptly enlarged, widened ventrally and there with three low but lamelliform and longitudinal ridges, with obvious vertical ridges on the lateral faces dorsally for a number of segments, ending abruptly in 110th of 181 or 111th of 203 segments, still recognizable at 98th segment of one of the anterior fragments. Lateral typhlosoles low but lamelliform, beginning and ending abruptly, in xxiii–xxviii. Supra-intestinal glands lacking.

Dorsal blood vessel single throughout, bifurcating just behind or just under the brain. Ventral trunk complete, bifurcating just over the subpharyngeal ganglia. Extra-esophageal trunks median to segmental commissures, filled with blood anteriorly but empty and unrecognizable posteriorly. Supra-esophageal trunk visible only in xi–xii. Subneural trunk unrecognizable and presumably lacking. Lateroparietal trunks unrecognizable. Segmental commissures of vi–x lateral, none found in v. Hearts of xi–xii, lateroesophageal (5 specimens).

Excretory system meronephric. A longitudinal band of closely crowded micronephridia is somewhat lateral to mV on each side of the body in iii–iv. Smaller clusters of nephridia are present on the anterior faces of septa 4/5–11/12 or 12/13. Nephridia are on the parietes from xiii posteriorly and behind the clitellum the loops are transversely placed. Nephridia almost certainly are in three longitudinal ranks on each side posteriorly, one rank about in *BC*, the other two further laterally. The medianmost tubule on each side in post-typhlosolar segments has a preseptal funnel.

Holandric. Seminal vesicles finely acinous, paired in xi and xii, in one worm smaller vesicles but with typical lobulation also present in ix. Male gonoducts of a side without epididymis, united just in front of 12/13, thence back apparently provided with a muscular sheath, zigzagged or shortly looped in xiv–xvi, slightly slenderer in xvii where they are lateral to the prostatic ducts, passing down into the parietes in the region of the insertion of 17/18 (but not traceable through the musculature). Prostates tubular,

coiled in xvii and xix, the posterior pair sometimes extending into xx or xxi. Ducts muscular, 1–2 mm. long. Penial setae to 1½ mm. long, slenderer than in the other species, shaft curved in an arc like the parentheses but somewhat asymmetrically, narrowing rather gradually toward ectal end to a thin and flat band with both margins curved over on concave side of shaft. Ornamentation of two longitudinal ranks of transverse serrations, one rank on the upper side of the shaft as it lies naturally on the slide and the other on the lower side. The serrations comprise 2–7 teeth of variable size and shape, some of a more or less triangular shape, others thorn-like. The functional setae are yellow and with each there is associated one small reserve seta.

Spermathecae with a main axis that is 2–3 mm. long, slightly and gradually narrowed entally, usually posteriorly directed on the ventral parietes and then upward on the anterior faces of the septa. One spermatheca turns mesially and anteriorly to pass into the segment next in front. The duct is much shorter than the ampulla which has on its inner wall numerous closely crowded annular ridges. Diverticulum a large, nearly circular dorsoventrally flattened disc on the parietes of the segment next in front of that containing the main axis and reaching well toward or even to the anterior septum, with a number of small seminal chambers. Ovaries fan-shaped and with several egg strings.

Reproduction. Iridescence is recognizable on the male funnels but is slight on those of the clitellate worm. Iridescence also is recognizable in the seminal chambers of the spermathecal diverticula of aclitellate specimens. Reproduction, inasmuch as sperm are matured and exchanged in copulation, is assumed to be biparental.

Remarks. A posterior portion had been torn off from three worms. Some intestinal caeca may have become unrecognizable because of softening and alcoholic browning in three of the dissected specimens. The penial setae usually were broken, without ectal portions or with tips softened, and obviously more or less deformed.

Only one calciferous sac is present in x of one specimen, no slightest trace of a sac is recognizable on the other side. Hearts of xi (1 specimen) and xii (another worm) at first appeared to be absent. The associated septum, in each case, was adherent to the gut in front of the hearts as if normally inserted there. The male gonoducts of one worm, though in contact in xii, obviously do not unite until well into xiii.

As the spermathecal pores are not minute they may, when fully open, be large enough to permit insertion of protuberances of the male field functioning as temporary intromittent organs.

A testicular chamber was not recognized, possibly because the peripheral union of the bounding septa became unrecognizable as the worms were opened and pinned out.

These specimens appear to differ from the type of *R. eiseni* (*cf.* below) as follows: Saddle-shape of clitellum (annular but thinner ventrally) that reaches to xx/2 (instead of only slightly into xix). Absence of genital markings at 14/15, 15/16, 21/22–25/26, and possibly also presence of a transverse row of circular areas within each marking. Presence of calciferous sacs, especially in xi–xii. Presence of intestinal caeca. Presence of seminal vesicles in xi and occasionally in ix. Orientation and location of the spermathecal diverticulum, *i.e.*, flattened on the parietes of the preceding segment (not vertically placed on the anterior face of the duct and perhaps in the same segment as the main axis of the organ). Individual variation as to number of genital markings is, of course, to be expected, but such very little data as now are available suggest specific uniformity as to shape and size of the clitellum in this genus. Intestinal caeca should have been recognizable if present in the type of *R. eiseni,* as it was well preserved, but they may have been overlooked or even considered to be unworthy of mention. Possibly some deformation or a peculiar reaction to preservation rendered the calciferous sacs unrecognizable. (For other comments see notes on *R. eiseni* below.)

Somatic characters show that *R. strigosa* belongs in the "*guatemalana*" group to which *R. eiseni* probably will have to be added. Possibly only early stages in development of the testicular chamber, or none at all, are to be found in a holandric section of the group.

Ramiellona mexicana Gates, new species.

Mexico, Dos Rios, Tehuantepec, January, 1900, 0–1–1. P. M. King (Eisen collection).

External characteristics. Length, 96 mm. (aclitellate worm), 116 mm. (clitellate specimen which lacks a posterior portion presumably torn off before preservation). Diameter, 7 mm. (clitellate worm). Segments, 253 (aclitellate), 195 + (clitellate). Pigmentation not determinable (alcoholic preservation, specimens browned). First segment soft, longitudinally furrowed, almost wholly withdrawn into the interior but intersegmental furrow 1/2 recognizable just behind the anterior end of body. Prostomium presumably to be considered prolobous, also withdrawn out of sight but firm (not soft like peristomium), much wider than long, with a deep groove marking off a circular area at center of which is a deep pit. Secondary furrows two per segment behind clitellum. Setae unrecognizable on ii and probably lacking, small, very hard to see even when tips are protuberant from the epidermis, ventral setae paired and in regular ranks but dorsal setae in irregular ranks in preclitellar segments, posteriorly all ranks irregular and arrangement becoming quincunxial. Apertures of ventral follicles of viii–ix about at same level as spermathecal pores and hence only slightly behind intersegmental furrows,

not in line with *a* and *b* ranks of other segments. Nephropores unrecognizable and apparently microscopic. First dorsal pore at 11/12 (2 specimens).

Clitellum saddle-shaped, dark red, reaching down to *B*, on xiv-xxii. A median region between the ventral borders of the clitellum is slightly depressed. The same region, in xv–xx of the aclitellate worm, is deeply depressed and so that the floor is invisible.

Spermathecal pores minute, superficial, obviously behind 7/8 and 8/9, unpaired and median. Female, male, and prostatic pores unrecognizable, the female pores possibly at *A*. Seminal groves unusually fine, shaped like parentheses, between equators of xvii and xix, at *B*. Slight tumescences at each end of the grooves may contain prostatic pores.

Genital tumescences areas of slight epidermal thickening, without distinct boundaries, paired in vii around apertures of *ab* follicles, unpaired and reaching beyond *B* in viii and ix where the posterior intersegmental furrows are irregularly met. A tumescence in each of segments xxvi–xxxii (clitellate worm) reaches laterally on both sides to *B* and anteroposteriorly to the intersegmental furrows.

Internal anatomy. Septum 4/5 membranous, 5/6–9/10 rather thickly muscular and funnel-shaped, 10/11–11/12 slightly strengthened. Septal insertions on the parietes do not correspond to the intersegmental furrows, 9/10–14/15 crowded together so that the coelomic cavities of ix–xiv are short.

Gizzard large and strong, with thick cuticular lining, in v. Four wide and strong muscle bands from the posterior end of the gizzard dorsally pass back at least to 12/13. Other and more numerous bands from the septa to the parietes are shorter. Esophagus deeply constricted at the septal insertions and markedly moniliform through ix–xiv, in each of those segments short (especially so in xiv) and, relative to width of body, narrow. A thick typhlosolar ridge is present at mV. Thin, vertical, and presumably calciferous lamellae with free median and dorsal margins are attached to floor and lateral walls but leave slightly roughened roof of the gut free. Intestinal origin seemingly in xvi (but possibly in xv?). Typhlosole very rudimentary or lacking until about xxx, thence fairly high, lamelliform but with slight vertical ridges on lateral faces, ending effectively in 132d segment (clitellate worm) though a very small and round rudiment is recognizable in the next twenty metameres. Caeca and lateral typhlosoles were not recognized and may be absent. Supra-intestinal glands lacking.

Dorsal blood vessel single throughout, traceable anteriorly to the brain and presumably complete (though bifurcations to ventral trunk were not recognized). Ventral trunk not visible in front of ix. Supra-esophageal trunk double in part and apparently not continuous, recognizable only in xii–xiii. Extra-esophageal trunks median to segmental commissures, recognizable only in vi–viii. No subneural trunk. Latero-parietal trunks unrecognizable. Seg-

mental commissures of v–x lateral (both specimens), those of v anterior to the gizzard, those of the other segments on anterior faces of the septa, traceable to the ventral trunk only in ix–x. Hearts of xi–xiii (both specimens) rather small but obviously latero-esophageal.

Excretory system meronephric. A large horseshoe-shaped cluster of micronephridia is present on the anterior face of 4/5. A fairly thick duct, recognized only on one side of one specimen, passes forward on the parietes into segment ii. Very small clusters of micronephridia are present on the parietes in iii, v, and posteriorly. Nephridia of postclitellar segments seemingly in six longitudinal ranks on each side. The median-most tubule on each side, in posterior segments of the body, is much thicker than the others and is provided with a slightly glistening preseptal funnel.

Holandric, testes manicate. Male funnels large in aclitellate worm but smaller in the other, plicate. Male gonoducts very slender, looped or zigzagged just behind the funnel septa, not traceable after reaching the parietes. Seminal vesicles vertical bodies on posterior faces of septa 10/11 and 11/12, medium-sized or smaller, acinous, and with many lobules. Prostates two pairs, coiled in xvii and xix. Ducts slender but with muscular sheen, ca. 4 mm. long. Lumen in glands slit-like in cross section, much smaller and circular in the ducts. Penial setae and enlarged setal follicles were not found in xvii–xix. Parietes covered, in xv–xx, by numerous diagonal muscle bands presumably responsible for depression or grooving of ventrum in the clitellar region.

Spermathecae long enough to reach up above gut, rather slenderly club-shaped, without external or internal indication of demarcation into ampulla and duct, very much narrowed in the parietes. The anterior spermatheca (both specimens) reaches forward into vi and has two diverticula. Two spermathecae are present in ix or anteriorly, each with its own diverticulum, the ducts (both specimens) united within the parietes. The diverticulum which passes to the anterior face of the duct at the parietes is short and rather digitiform. The axial lumen, located on the side of the diverticulum next to duct, opens into six discrete seminal chambers. Ovaries small, fan-shaped, with numerous short egg strings.

The ventral follicles of vii–ix are very thick but protrude only slightly into the coelomic cavities. Setal shafts without nodulus, curving slightly to one side near ental end. An ectal portion of each seta (clitellate specimen) is lacking as is ornamentation on the remaining portions.

Reproduction. Spermatozoal iridescence on the male funnels is limited to a peripheral region central to which the funnels are very dark, not black but with a reddish tinge. The color does not appear to be due to blood. Iridescence is unrecognizable in the spermathecae. Nevertheless, there are in the ampullary coagulum small bundles of fine threads that may be spermatozoa.

Small, spindle-shaped to ovoidal bodies of a definite red color are scattered through the coagulum that fills the seminal chambers of the spermathecal diverticula. If, as seems possible, these red bodies contain sperm, then a massive aggregation may have been present on the male funnels. Reproduction, in absence of evidence to the contrary, is assumed to be biparental.

Ingesta. Soil.

Remarks. These worms had been crowded into a too-short container. The epidermis of xiv, because of the folding over of the specimen, had been creased and then cracked so that the females pores could not be found. The gut of one worm may have been ruptured during study of external characteristics. The second specimen was dissected before examination of external characters, but the gut already was ruptured in the region of xxx.

Some sort of genital markings probably are present in *BB* of the clitellar region, but even after soaking in picric acid solution optical differentiation was too poor to permit any attempt at characterization.

Clitellar tumescence is unrecognizable externally on the worm called aclitellate though some thickening of the epidermis is noticeable at the middorsal incision. Sperm obviously had been matured and the worm almost certainly had copulated. Accordingly, one more must be added to the lengthening list of specimens that have matured sperm and copulated though aclitellate.

No indications of existence of a testicular chamber were recognized, but absence cannot be asserted.

Some of the somatic anatomy obviously is like that of the "*guatemalana*" group: Retraction of the prostomium and derogation of the peristomium associated with loss of setae at least in ii. Small size and close pairing (ventral ranks only) of setae anteriorly. Location of the first dorsal pore. Presence of all septa from 4/5, enlargement into posteriorly directed funnels of 5/6–9/10, marked muscularity in 6/7–9/10. Primitive location of gizzard, in v. Postgizzard portion of esophagus short and slender. Presence of calciferous lamellae in ix–xii. Presence of an intestinal typhlosole. Hearts of x lateral, of xi–xii latero-esophageal. Absence of a subneural vessel.

Differences from the "*guatemalana*" group are as follows: Anterior dislocation of the apertures of the ventral follicles of viii–ix. Development of tumescences (associated with intraparietal glands?) around the apertures of the ventral follicles in vii-ix, enlargement of those follicles (and development of copulatory setae?), abortion of ventral follicles in xvii–xix. More posterior intestinal origin. Presence of hearts in xiii (and of segmental commissures in v?). Union of the spermathecae midventrally. Minute size of spermathecal pores. Some of those differences have been found elsewhere within generic limits and now seem likely to be of minor taxonomic importance.

Evolution of the calciferous portion of the esophagus and of the excretory system in the anterior segments has been proceeding in ways that were not involved in the ancestry of the "*guatemalana*" group. Common origin with that group now appears to have been sufficiently remote to require generic distinction when adequate characterization of structure is possible.

Ramiellona eiseni (Michaelsen).

Eodrilus eiseni Michaelsen, 1911, Zool. Jahrb. Syst. 30, 559.

This species was erected on a single specimen from Huehuetenango. The importance attached to somatic organization in the classical system is shown by the characterizations of two systems: excretory organs meganephric, dorsal blood vessel single, last hearts in xii. The meganephry required the species to go in an Acanthodriline genus but micronephridia were later found (Pickford, 1937) in a small piece (now in the U.S.N.M.) of the body wall from the type. Pickford's transfer to *Howascolex* was qualified by a "?" because of absence of calciferous sacs. A widening of the gut in xii-xiii was attributed by Michaelsen to flattulence, but might have been due to distention by ingesta that was passing through at time of preservation. Poor preservation may have been responsible for failure to detect calciferous lamellae (the gut of earthworms sometimes is in very poor condition even though peripheral anatomy seems to be well preserved.)

The species obviously is holandric, presence of sperm on male funnels fortunately having been recorded. Absence of seminal vesicles in ix and/or xi is unusual as their disappearance would be expected to follow rather than to precede metandry. Spermathecal pores were said to be small but what that means is unknown as size usually was not mentioned. Location of male pores also was not stated. Except for absence of calciferous sacs, *P. eiseni* now seems to be close to *R. strigosa*. If that is correct, both species probably share with others of the group certain unrecorded characters.

Ramiellona irpex (Michaelsen).

Eodrilus irpex Michaelsen, 1911, Zool. Jahrb. Syst., 30:555.
? Acanthodrilus irpex Michaelsen, 1925, Mitt. Zoll. Mus. Hamburg, 41:76.

Eodrilus irpex was erected on a single specimen from Huehuetenango that was provided (like the type of the previous species) by Eisen. Size of spermathecal pores, location of male pores, intestinal caeca, typhlosole and even the andry were not mentioned in the description. The species may be metandric but with retention of anterior male funnels as in *R. tecumumami* and *R. guatemalana,* or holandric but with only one pair of seminal vesicles as in *R. eiseni*. A supposedly meganephridial excretory system, as in *R.*

eiseni, was found (Pickford, 1937) to be micronephridial, *i.e.*, meronephric but nothing is known about the tubules of the preclitellar region of the body where generic peculiarities are likely to be more obvious. Calciferous lamellae are present in xii but in viii–xi are within paired, dorsally directed and discrete glands with slender stalks that open into the gut close to mD. The spermathecae are much like those of *R. balantina*.

Acanthodrilus irpex was described from a specimen from Mexico which is larger than the Guatemalan worm and has paired genital markings. Segment number is more than twice that of the type, but a clitellum had not been developed. No information as to internal organization was recorded though the worm presumably was opened to enable generic identification. In view of the external differences conspecificity with the type requires confirmation.

Ramiellona tecumumami (Michaelsen).

Eodrilus tecum-umami Michaelsen, 1911, Zool. Jahrb. Syst., 30:550.

This species was erected on specimens from Huehuetenango that were provided by Eisen. Size of spermathecal pores, location of first dorsal pore and of male pores, intestinal origin, and caeca were not mentioned. In the usual classical manner, location of the last pair of hearts is all that was recorded about the vascular system. As in case of the two preceding species, a supposedly meganephridial excretory system was later found (*cf. R. vulcanica* below) to be micronephridial. Unfortunately, no further information as to the type or other specimens was vouchsafed. Omissions in the list of differences between *R. tecumumami* and *R. vulcanicus* warrant assumptions that spermathecal pores are large, that the male pores are in seminal grooves at level 17/18, that calciferous lamellae are present and especially large in xi–xii, that intestinal caeca are present, that there are vascular commissures or hearts in viii-xii. Spermathecae appear to be erect in coelomic cavities. Spermathecal pores are median to *A*, more so at 8/9. A continuation of the process that apparently is under way can be expected to result in median union of the paired organs, first at 8/9 rather than at 7/8 as in *R. mexicana*.

Ramiellona stadelmanni Michaelsen.

Ramiellona stadelmanni Michaelsen, 1934, Mitt. Zool. Mus. Hamburg, 45:53.

This species is known only from the original description of two internally macerated specimens from Honduras. Reproductive apertures (except the female pores) and seminal grooves were not seen. Septum 5/6, the intestinal

origin, and intestinal caeca were not mentioned. One part of the setal formula appears to be incorrect, in

$$AA = \frac{5}{6} - \frac{6}{6} AB,$$

BC presumably should be read for AB as setae are closely paired anteriorly.

Whether the spermathecal pores are minute or merely unrecognized because of strong contraction is unknown but no porophores or special protuberances are shown in a figure of the male field. Presence of seminal vesicles in xi–xii usually is associated with holandry which is assumed in order to include this species in the key below. Relationships indicated by the genital markings, calciferous portion of the gut, the large hearts of xi–xii, and other structure, in absence of information about insertion of 5/6 (which may have been membranous and destroyed in pinning out or even in handling the specimen), is believed to warrant assuming that the gizzard is in v. Intestinal caeca (as in some of the author's specimens), possibly even calciferous sacs, may have been unrecognizable because of the internal maceration.

Ramiellona americana (Gates).

Ramiella americana Gates, 1957, Breviora, 75:1.

This species was erected on a single, probably incomplete, specimen supposedly from Guatemala. The esophagus is slender behind the gizzard but if calciferous sacs and lamellae are present in this species they had become unrecognizable because of internal maceration. Spermathecal pores are large enough to admit protuberances functioning as temporary intromittent organs. The lateral typhlosoles, intestinal caeca, lateral hearts of x, lateroesophageal hearts of xi-xii, the testicular chamber and the spermathecae suggest relationships to a "*guatemalana*" group of species. From that group, however, *R. americana* is set apart by the nephridia of the anteriormost portion of the body.

Ramiellona lasiura (Graff).

Howascolex (Graeeevelynia) lasiurus Graff, 1957, Senckenbergiana, 38:129.

This species was erected on 3 specimens (2 juvenile) from Salvador. The description is in the best classical tradition. Accordingly, though the typhlosole was well characterized, information as to size of spermathecal pores, GM glands and lateral typhlosoles, kind of hearts, trunks of the circulatory system, nephridia of the preclitellar region, testicular chambers, etc., is not to be expected. Gonads were not seen and perhaps also the gonoducal funnels as the latter were not mentioned. The number of seminal vesicles also is un-

known. Possibly masses of coagulum (which have been mistaken for vesicles in the past) were what was seen in segment xi. A single pair of vesicles, in xii, usually is indicative of metandry but in *R. eiseni* is associated with holandry. Hence, the andry is unknown, but to enable inclusion of "*lasiura*" in the key, metandry is assumed. Inability to recognize gonads and perhaps also the enteric insertion of septum 5/6 may have made recognition of axial location of certain organs difficult (though level of entrance of spermathecae into the parietes should have provided one good clue). If the gizzard is in v rather than in vi, other organs also will prove to be located as in *R. guatemalana* and a testicular chamber may well be present. Restriction of hearts to vii–xi and presence of calciferous sacs in ix–xiii certainly require confirmation.

Ramiellona sauerlandti (Graff).

Howascolex (Graceevelynia) sauerlandti Graff, 1957, Senckenbergiana, 38:131.

This species was erected on 2 specimens (1 juvenile) from Salvador (*cf.* comment on description of *R. lasiurus*). Male pores, gizzard, calciferous sacs, intestinal origin and hearts appear to be as in *R. guatemalana*. Perhaps, then, the typhlosole which was not characterized also is of the same sort and associated with intestinal caeca. Spermathecal pores were not recognized and may be minute—protuberances in region of prostatic pores apparently lacking. Except for presence of hearts in xi–xii, nothing is known of the vascular system and the anterior nephridia are not characterized. Male funnels are said to be in xi–xii which in itself is very unlikely but becomes even more so when seminal vesicles are in xi–xii. A *lapsus calami* doubtless is responsible for an erroneous location of the testes. The holandry then suggests relationships with *R. strigosa* and *R. stadelmanni*.

Ramiellona vulcanica (Graff).

Howascolex (Graceevelynia) tecumumami vulcanicus Graff, 1957, Senckenbergiana, 38:127.

This form was erected on 6 specimens (5 subadult) from Salvador. As usual, information as to the vascular system and nephridia of a preclitellar region is lacking. The level of insertion of septum 5/6 on the gut apparently was not determined as the gizzard was said to be in v or vi (v in *R. tecumumami*). Graff examined the type of this species and found the excretory system to be micronephridial, *i.e.*, meronephric but did not record other important information that could have been obtained at the same time.

Among the differences between the Salvador and Guatemala worms respectively, are the following: Length 140 to 180 mm.—440 to 1000 mm. Di-

ameter, 7 to 9 mm.—9 to 12 mm. Segments, 260—360 (+ ?). Spermathecal pores, in *AB* (possibly not minute)—median to *A* (possibly minute). Genital markings, present at 16/17 and 19/20—lacking. Septum 10/11, lacking —present. Intestinal caeca, present—lacking (?). Penial setae, 2.6 mm. long—4 to 4.5 mm. long. Spermathecae, with a large round diverticulum on the ampulla (?)—adiverticulate but with seminal chambers sometimes recognizable in a small, transverse protuberance near ental end of duct. More information is needed about important somatic anatomy to determine relationships of the two forms not only to each other but also to the rest of the species whether holandric or metandric.

Discussion

Certain species do or probably do share with "*guatemalana*" many if not all of the following characters: Peristomium, flaccid and usually more or less retracted into anterior end. Prostomium, prolobous, not flaccid though usually retracted. (Associated with the retraction there seems to be a tendency to abort the setal follicles in the anteriormost segments.) Setae, small and closely paired, at least anteriorly, ventral setae of xviii retained, ventral couples of xvii and xix penial. First dorsal pore in region of 11/12–12/13. Spermathecal pores, in *AB* at 7/8–8/9, not minute, large enough for insertion during copulation of temporary protrusions from the male field. Male pores, at 17/18 and in seminal grooves that are lateral to *B*. Genital markings, unpaired, median, at intersegmental furrows, usually if not always with a single transverse row of small circular areas. Septa, present from 4/5, 5/6–9/10 funnel-shaped, 6/7–9/10 thickly muscular, 10/11–11/12 peripherally fused except ventrally to form a testicular chamber. Gizzard, in v. Calciferous lamellae, in viii–xii, in sacs (4 species) that are somewhat more distinctly constricted off from the gut in xi–xii. Intestinal origin, near insertion of 14/15. Intestinal caeca, paired, from dorsum in some of xx–xxx. Typhlosole widened ventrally and with three longitudinal ridges. Lateral typhlosoles present in region of xx–xxx. Hearts, of x lateral, of xi–xii lateroesophageal. Dorsal blood vessel, single throughout and complete. Extra-esophageal trunks median to hearts and segmental commissures. No subneural trunk. Nephridia of iii–iv (presumably astomate) closely crowded in two longitudinal bands parallel to the nerve cord. Astomate micronephridia on anterior faces of septa in next eight segments in each of which there is one pair of nephridial ducts.

Some such uniformity of structure must be shared by species so closely related as to belong in a monophyletic genus. However, some of the characters just listed may not be available to define even the genus in which *R. guatemalana* belongs. Calciferous sacs of xi–xii, for instance, distinguish four species of a "*guatemalana*" group from *Ramiella* but other species, obvi-

ously of the same group, seemingly have no sacs. The excretory system in the first few segments of *R. americana* and *R. mexicana* provides differences from the "*guatemalana*" group that may be significant at generic level but not necessarily so from the unknown structure in most species of *Ramiella*. The calciferous section of the gut appears to deny close relationship between *R. americana* and *R. mexicana* as well as of both to the "*guatemalana*" group. Most divergent, possibly, is *R. irpex* which certainly is generically distinguishable by its calciferous glands alone from *Ramiella*. Nothing is known, however, about an anterior portion of the excretory system in *R. irpex*. Relationships of the latter to other American species accordingly are uncertain.

Ramiellona obviously is a congeries, as a whole morphologically indistinguishable from *Ramiella* and presently incapable of segregation into natural generic units. The group may well prove to be a most important constituent of the native earthworm fauna in a region from the isthmus of Tehuantepec to Nicaragua.

Eisen long ago suggested that exotic species were replacing the natives in Mexico and Central America. If, as elsewhere, endemics are haemerophobic they should be sought in undisturbed soils, especially in jungles (which must exist even today in considerable areas) and preferably near or at end of the rainy season when mature individuals are most likely to be easily obtainable.

Key to Species of Ramiellona

1. Stalked calciferous glands lacking 2
   Slender stalks of calciferous glands pass to gut close to mD in viii–xi ..... *R. irpex*[2]
2. Spermathecal pores paired 3
   Spermatheca pores unpaired, at mV ..... *R. mexicana*
3. Holandric[3] 4
   Metandric 7
4. Spermathecae adiverticulate 5
   Spermathecae diverticulate 6
5. Clitellum annular, genital markings paired ..... *R. sauerlandti*
   Clitellum saddle-shaped, genital markings unpaired ..... *R. stadelmanni*
6. Spermathecal diverticulum dorsoventrally flattened in preceding segment ..... *R. strigosa*
   Spermathecal diverticulum vertical and on anterior face of duct ..... *R. eiseni*
7. Setae in lumbricin arrangement posteriorly 8
   Setae in quincuncial arrangement posteriorly 11
8. Spermathecae without a posterior growth curvature 9
   Spermathecae with a posterior growth curvature[4] 10
9. Spermathecal pores median to *A*[5] ..... *R. tecumumami*
   Spermathecal pores in *AB* or centered at *A* ..... *R. vulcanica*
10. Quadripostatic, quadrithecal ..... *R. americana*
    Biprostatic, bithecal ..... *R. balantina*

11. Clitellum, saddle-shaped, on xiv–xix, spermathecae adiverticulate ..... *R. guatemalana*

Clitellum annular, on xiii–xx, spermatheca with rosette-shaped diverticulum ..... *R. lasiura*

Note, there is no couplet 12.

2. Guatemalan and Mexican worms referred to *R. irpex* may be specifically distinct.

3. Andry of some species is unknown, compare notes above on *R. irpex* and *R. lesiura*.

4. In this state the ampulla appears to be an outgrowth from the posterior face of the duct.

5. *A, B, C, D* are meridians of longitude passing across apertures of *a, b, c, d*, setal follicles respectively. mD and mV, respectively, indicate mid-dorsal and midventral. eq indicates equator. C is the abbreviation for circumference (U in German). *AB* is the meridional space between *A* and *B*.

Family MEGASCOLECIDAE

This family was recently redefined (Gates, 1959) to exclude all genera except those with racemose prostates of the pheretima sort.

Genus **Pheretima** Kinberg, 1867

Pheretima diffringens (Baird, 1869).

Guatemala, Totenicapan, 0–3–2. (Doubtless collected by Eisen during his explorations, possibly in May–Nov., 1902.)

The prostate glands are lacking, in one of the clitellate worms, but the prostatic ducts are well developed. The dissected individual (and probably the others also) is of an intermediate morph evolving in direction of the anarsenosomphic stage. Reproduction is parthenogenetic.

The species is of Asiatic origin and may have been introduced to Guatemala by the Spaniards.

Family GLOSSOSCOLECIDAE

This family is now restricted in accordance with Michaelsen's later classifications (*cf.* Gates, 1959).

Genus **Pontoscolex** Schmarda, 1861

Pontoscolex corethrurus (Müller, 1857).

Guatemala, Totenicapan, 0–0–2. (Doubtless collected by Eisen during his explorations, possibly in May–Nov., 1902.)

Two unlabelled tubes, but part of the Eisen collection, almost certainly are of the same species and may have been collected at the same time. Specimens were in an advanced stage of maceration.

Seminal vesicles, when recognizable, small and coiled up in xii.

Spermatozoal iridescence is lacking on male funnels and spermathecae are juvenile or if larger are empty in worms with clitellum at maximal tumescence.

Reproduction is parthenogenetic.

The species is of American origin, but is likely to have been introduced to Guatemala, possibly after the Spanish conquest.

Family SPARGANOPHILIDAE

Genus **Sparganophilus** Benham, 1892

Sparganophilus eiseni Smith, 1895.

Eisen collection, 0–1–16. (No further data.)

External characteristics. Length, to 140 mm. Diameter, in clitellar region, to 2 mm. Segments, 210 (posterior amputee?), 231, 257. Anus dorsal (four specimens) or terminal (posterior amputees). Prostomium, zygolobous (14 specimens). Peristomium with a transverse furrow in *DD* immediately in front of the equator (14 specimens) and often at the equator a ring of very small spots some of which occasionally look much like tips of setae. Setae *c* and *d* dorsal throughout, ventral setae of clitellar segments with nodulus much nearer ectal end and, further ectally, three to seven irregular circles of very small teeth. Clitellum, red, covering xvi–xxv, intersegmental furrows 16/17–24/25 obliterated, dorsal setae of those segments lacking. The anterior and posterior margins are not distinguishable externally but the red coloration extends through xv and xxvi, often into xiv and through xxvii but 14/15, 15/16 and 26/27 are not obliterated and the epidermis is less thickened. Tubercula pubertatis, broad bands just lateral to *B* in which the red clitellar coloration is lacking, extend from 17/18 or eq/xviii to eq/xxiii or to 23/24. A median portion of the band is translucent, the lateral portion of a brilliant white opacity which is often continued as a narrower strip to eq/xvii and eq/xxiv. Apertures of genital glands (sometimes called prostates), on very small white protuberances, always just lateral to *b*, on xvi–xvii (16 specimens), xxiv–xxvii (14), xxiv–xxvi (1), xxv–xxviii (1).

Internal anatomy. Last hearts in xi (5 specimens). Anterior lateroparietal trunks, two pairs. The larger of each pair passes up on the anterior face of 13/14 (1 specimen) or 14/15 (4) to join the dorsal trunk.

Nephridia are lacking in xii and anteriorly but are present in xiii, probably also in xiv though very small, larger in xv–xxvii, much larger still from xxviii. Nephridial vesicles are lacking and the very slender duct passes into the parietes in *AB*, close to or almost at *A*.

Male funnels, large and plicate. Seminal vesicles, medium sized or smaller, in xi–xii, filled with very dark and almost black matter.

Spermathecal duct longer than the ampulla, with muscular sheen, slightly narrower in entalmost portion. Ovaries, narrow, discoidal, terminating distally in a single egg string (5 specimens) which may contain as many as five ova. Ovisacs, small, lobed, on posterior face of 13/14.

REMARKS. Nephropores and male pores are unrecognizable. Except as otherwise indicated above, external characteristics and anatomy are as in Florida specimens (Gates, 1943, p. 94).

Spermatozoal iridescence is lacking (5 specimens) on male funnels and in spermathecal ampullae which appear to be shrunken. Only two mature ova are left in one ovary which has an eggless egg string. These worms may have been preserved at or near the end of the breeding season.

The genitalia of earthworms are now known to be liable to rapid evolutionary modification. The ovaries obviously are the most conservative of the reproductive organs. Accordingly, the similarity of sparganophilid and lumbricid ovaries may prove to be of importance in estimating relationships of a family so divergent that consideration of its phylogeny alone was omitted by Stephenson (1930) in his monograph.

Family LUMBRICIDAE

Genus **Bimastos** Moore, 1893

Bimastos parvus (Eisen, 1874).

Guatemala, Totenicapan, 0–0–3. (Doubtless collected by Eisen during his explorations, possibly in May–Nov., 1902.)

Diameter, *ca.* 1.5 mm. Clitellum (xxiii?) xxiv–xxx (2 specimens), xxiii–xxx (1).

The species is exotic in Guatemala but its original home, usually thought to be in North America, is unknown.

Genus **Dendrobaena** Eisen, 1874

Dendrobaena rubida (Savigny, 1826).

Guatemala, Totenicapan, 2–0–8. (Doubtless collected by Eisen during his explorations, possibly in May–Nov., 1902.)

Diameter, *ca.* 1.5 mm. Clitellum (xxv) xxvi–xxxi (xxxii?), three specimens, xxvi–xxxi five specimens. Tubercula pubertatis, in xxix–xxx, just lateral to *B*, distinctly outlined but TP glands lacking at least in coelom (3 specimens). Atrial glands are present (3 specimens) but there are no supraparietal glands associated with the genital setae (*a* and *b*) of xvi. Athecal (2 specimens), rudimentary spermathecae opening at 10/11 (1 specimen). Spermatozoal iridescence on male funnels is slight.

The species is of European origin and may have been taken to Guatemala by the Spaniards soon after colonization began.

California Earthworms and Their Method of Reproduction

The earthworm fauna of California comprises more than twenty species, precise enumeration impossible because of uncertainty as to status of several taxa. Even if all endemics (indicated by asterisk in the list below) are valid species, which now seems unlikely, the lot will constitute less than a third of the number present in the state. Natives once were "most common" (Eisen, 1894, p. 41) but by the end of the century (Eisen, 1900, p. 249) finding them in gardens and other places where earthworms are mostly likely to be sought had become "almost impossible." Nearly forty years later, efforts to secure material from sites recommended by Eisen (1900, p. 249–250), undisturbed soil in gulches and mountain meadows, under rotten stumps and decaying leaves in the forest, yielded only seven specimens (Gates, 1941) of a single indigenous species. If Eisen's prophecy that eventually few if any native species will be left is not already fulfilled, conservation, at least as museum specimens and from as many sites as possible, ought to be provided at once. Native species are protected in Australia and export, even for scientific study, is restricted. In California, the competitive exotics are widely distributed by organic gardeners and anglers, by the latter perhaps in the very places most likely to harbor native remnants. How massive that distribution may have become during the last twenty or so years can only be guessed but it is noteworthy that in 1958 expenditure of a little time and money already had revealed Californian addresses of 207 individuals or firms engaged in raising or distributing exotic earthworms, or both.

Among the factors favoring exotic supremacy, according to Eisen, are much longer breeding periods and resistance to human disturbance of habitats. Much remains to be learned about seasonal activity, in California, of every kind of earthworm but endemics of many areas rather generally are believed to be haemerophobic. Exotics, and more especially the European lumbricids, obviously are not haemerophobic and even are called haemerophilic.

More recently parthenogenesis has been thought to favor colonization of new areas. However, biparental reproduction is obligatory (OB, in the list) for five introduced lumbricids including the one raised by most "earthworm farmers." Biparental reproduction is very probable (pB) in one European and in two of three Asiatic exotics. Seven exotics admittedly are parthenogenetic (P), as very probably (pP) are four others, but only one of the eleven now seems likely to be as common as the sexual peregrines.

Acquisition of the ability to reproduce parthenogenetically often has been followed, in earthworms, by evolution of genital polymorphism. Athecal

morphs of three European exotics are known and may be present in California. Sperm are matured and then exchanged during copulation by individuals of one thecal morph of *D. rubida* in which parthenogenesis is facultative. One California endemic (*Plutellus papillifer*) also is polymorphic but whether parthenogenesis is possible in individuals that mature and exchange sperm remains to be determined. Another endemic (*Plutellus umbellulariae*) with 2, 3, or 4 pairs of spermathecae may have evolved a similar sort of polymorphism. Sperm are matured and exchanged by individuals of some morphs but of which ones was not recorded. Spermathecae are, of course, much more likely to be deleted than added. The ancestral hermaphroditic morph, then, may be octothecal. Nevertheless, a sexthecal morph of the usually (and presumably normally) quadrithecal *rosea* was found by McKey-Fender in Oregon.

Biparental reproduction is very probable in worms that mature and exchange sperm but there is at present no evidence to prove that it is obligatory in any native species.

List of California Earthworms

(Endemics are marked by asterisks)

Ocnerodrilidae	*Ocnerodrilus occidentalis*	pP
Acanthodrilidae	*Microscolex dubius*	pP
	Microscolex phosphoreus	pP
	**Plutellus collinus*[6]	
	**Plutellus fenderi fenderi*[6]	pB
	**Plutellus marmoratus*	pB
	**Plutellus papillifer*	pP and pB
	**Plutellus sierrae*[6]	
	**Plutellus umbellulariae*[6]	pB and P?
Octochaetidae	*Diehogaster bolaui*	
	Diehogaster saliens	pB
Megascolecidae	*Pheretima californica*	pB
	Pheretima diffringens	P
	Pheretima hawayana	pB
Sparganophilidae	**Sparganophilus smithi*[6]	
	**Sparganophilus sonomae*[6]	
Lumbricidae	*Eiseniella tetraedra*	P
	Eisenia foetida	OB
	Eisenia hortensis	pB
	Eisenia rosea	P
	Dendrobaena octaedra	P
	Dendrobaena rubida	P and B
	Bimastos parvus	pP
	Allolobophora chlorotica	OB
	Allolobophora trapezoides	P
	Allolobophora turgida	OB
	Lumbricus rubellus	OB
	Lumbricus terrestris	OB
	Octolasium lacteum	P
(Eudrilidae)	*Eudrilus eugeniae*[7]	

6. Known only from the original description or material.

7. Unrecorded as yet from natural habitats but known to have been distributed to earthworm farmers in California.

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